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Intraspecific variation in external morphology of the American lobster, *Homarus americanus* (Crustacea: Decapoda: Nephropidae)

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Abstract.—Intraspecific variation in external morphology of *Homarus americanus* H. Milne Edwards was examined in order to interpret better the fossil record of clawed lobsters. Several hundred *H. americanus* were collected from the Gulf of Maine. Lobsters were collected from rocky, shelly and muddy substrates. Detailed examination of 175 specimens indicates that carapace proportions, carapace groove positions, expression of carapace spines and general claw form are virtually constant within the sample—regardless of age, sex or substrate. This corroborates the scarcely published conclusion of taxonomists on modern lobsters: these external features are, in fact, reliable species characters. This study also shows, however, that number and arrangement of spines on the rostrum and claws are variable within the species and, therefore, not good species characters; this variation is unrelated to age, sex or substratum.

The clawed lobsters have a fossil record extending back to the Permo-Triassic (ca. 250 m.y.a.). The extant family Nephropidae sensu Tshudy & Babcock (1997)—to which *Homarus* Weber, 1795 belongs—is known from rocks of Early Cretaceous age (ca. 130 m.y.a.). Observations on fossil lobsters are almost entirely limited to external hard part morphology. Interpretations of the taxonomy and evolution of fossil lobsters are, therefore, based exclusively on external hard parts, especially carapace groove pattern and aspects of carapace ornamentation. An understanding of intraspecific variation is fundamentally important to these interpretations but there is scant published information on intraspecific external variation in lobsters.

Templeton (1935) examined *H. americanus* H. Milne Edwards 1837 from four localities off New Brunswick and Nova Scotia, with the most widely separated locales being approximately 440 km apart. In lobsters approaching sexual maturity, he observed that the claws of males, and the width and thickness of the abdomen in females, increase at a greater rate than does body length. He also observed that these features vary geographically.

Saila & Flowers (1969) studied bathymetrically related external variation in *H. americanus* collected off Rhode Island by analyzing linear measurements of 16 external features, mostly aspects of the appendages and carapace. Using multivariate analyses, they found that inshore and offshore groups were distinguishable by "small shape differences," that these differences were more pronounced in females than in males, and they suggested that there may also be differences among geographically isolated subsets inshore. They also reported that females were relatively bulkier than males. Two of their 16 measurements, carapace length and maximum carapace width, were considered in the present study.

This study of intraspecific variation in *H. americanus* was conducted in order to better interpret the fossil record of *Homarus*-like lobsters. *Homarus*-like fossils have been collected from stratigraphic sections spanning millions of years; these collec-

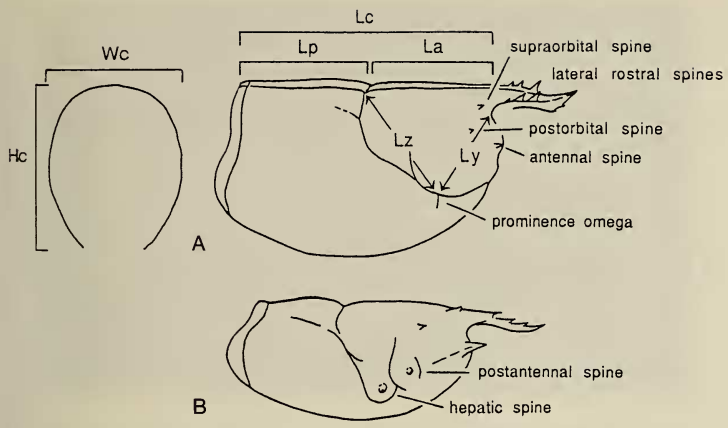


Fig. 1. Locations of carapace spines and orientations of measurements taken on: a, *Homarus americanus* H. Milne Edwards (posterior and lateral views), and b, *Hoploparia stokesi* (Weller). Abbreviations: Hc, carapace height; La, length of anterior portion of carapace; Lc, carapace length; Lp, length of posterior portion of carapace; Ly, distance between prominence omega and orbit; Lz, distance between prominence omega and dorsal end of postcervical groove; Wc, carapace width.

tions provide opportunities to examine lobster morphology through time. Interpretations of these potentially informative fossil collections have been limited, however, by lack of published information on intraspecific variation in modern lobsters.

Hoploparia McCoy, 1849 is a fossil genus considered ancestral to *Homarus* (e.g., Mertin 1941, Secretan 1964, Tshudy & Babcock 1997). In Antarctic (James Ross basin) *Hoploparia stokesi* collected over an area roughly 80 km in longest dimension, five external features are observed to display significant, stratigraphically related variation (Feldmann & Tshudy 1989, Feldmann et al. 1993). These features include: the morphology of the abdominal tergumpleuron boundary (which on geologically older lobsters bears a prominent boss but, on younger lobsters, bears an oblique ridge), the morphology of the thoracic region (which is more inflated on geologically older lobsters), hepatic and postantennal spines (which are present on geologically older lobsters), and general claw form (being more delicately constructed, less sculptured and more finely ornamented in geologically older lobsters) (Feldmann et al. 1993). In order to infer intraspecific or interspecific morphologic variability within these fossil *Hoploparia*, we examined the nature of intraspecific variation in the same or similar features in *H. americanus*.

Methods

Several hundred live *H. americanus* were collected from the Gulf of Maine in the vicinity of Mount Desert Island, Maine (from Stave Island to Sand Beach on Mount Desert Island, a distance of approximately 15 km) in May–June, 1995. The first 175 specimens were measured and otherwise examined in detail. Specific features examined include (Fig. 1): the proportions of the carapace and some of its regions, the presence or absence of three carapace spines (supraorbital, postorbital and antennal), the

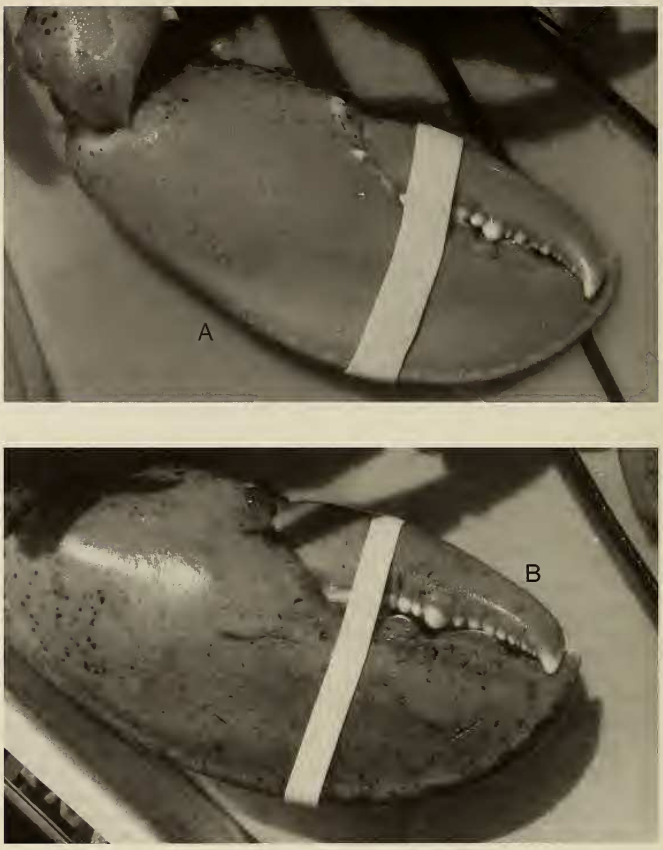
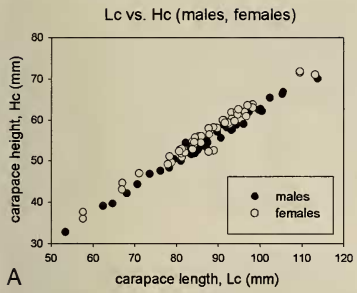
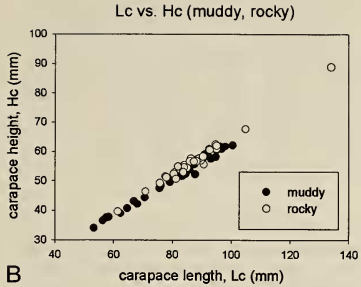
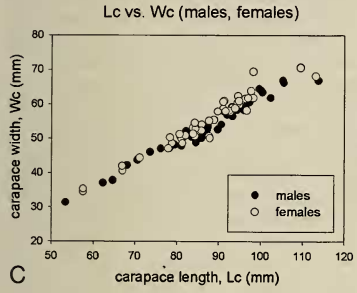


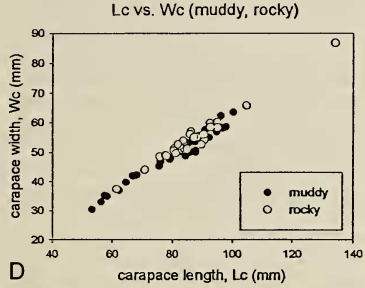
Fig. 2. Unabraded (a) and abraded (b) lower surface of claws on lobsters inhabiting muddy and rocky substrata, respectively.

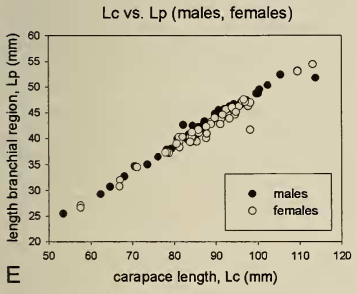
arrangement and number of rostral spines, and the arrangement and number of spines along the upper, inner margin and lower, inner margin of the palm (propodus) of cutter and crusher claws. Carapace length (Lc), height (Hc), width (Wc), and the distance from the posterior margin of the postcervical groove (Lp) (Fig. 1) were measured in order to gauge the volume of the thoracic region and, by implication, the branchial chamber. The distance from the prominence omega (mandibular external articulation) to the orbit (Ly), and to the postcervical groove on the dorsomedian (Lz) (Fig. 1), were also recorded in order to detect any variation in the proportions of the carapace.











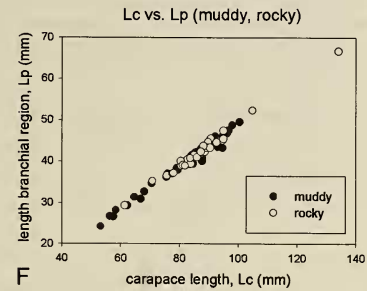


Fig. 3. Scatterplots of various measurements (carapace height, Hc; carapace width, Wc; posterior portion of carapace, Lp) versus carapace length (Lc). Plots indicate that measured features increase linearly through ontogeny and do not vary with sex or substratum.

Table 1.—Frequency of expression of postorbital spine in association with sexes and substrates.

# Postorbital spines	Overall $n = 148$	Male $n = 73$	Female $n = 75$	Mud dweller $n = 32$	Rocky dweller $n = 31$
Spine	66%	71%	60%	75%	71%
Spinule	29%	25%	33%	16%	29%
Absent	5%	4%	7%	9%	0%

Table 2.—Frequency of expression of antennal spines in association with sexes and substrates.

# Antennal spines	Overall $n = 150$	Male $n = 74$	Female $n = 76$	Mud dweller $n = 33$	Rocky dweller $n = 32$
2	8%	7%	9%	0%	16%
1.5	7%	7%	8%	6%	3%
1	84%	86%	82%	94%	81%
0.5	0%	0%	0%	0%	0%
0	1%	0%	1%	0%	0%

Each of these features/distances was examined with respect to age (proxied by carapace length), sex and substratum texture.

Water depth and substratum texture were recorded for each of the lobsters examined. Lobsters were collected from depths ranging from 6 to 50 meters. Substratum texture was interpreted from sonar reflection on a fathometer (American Pioneer Fishscope). Bottom grabs taken at several stations confirmed accuracy in interpreting bottom texture from the fathometer.

Dissolved oxygen for surface and bottom water samples was determined on-board by Winkler titration. Unfortunately, the hypothesis that "thoracic inflation (as observed in Antarctic *Hoploparia*) is an adaptation to living in less oxygenated environments" could not be satisfactorily tested in this study; dissolved oxygen just above the substratum varied insignificantly over the study area during the investigation.

Relationships between morphology and age, sex or environment were evaluated using univariate statistics. Methods included regression and Chi-square analyses.

Testing for any relationships between morphology and environment in *H. americanus* is complicated because many individuals of this species make an annual offshore–onshore migration. Many lobsters found in the study area during the summer spend the winter offshore in deeper waters and, presumably, on finer-grained and, probably, less-oxygenated bottoms. Therefore, collecting a lobster from a particular location is no guarantee that the lobster spent its life, or any large amount of time, there. Fortunately, the substrate a lobster has inhabited, at least since its last molt, can be determined by examining the lower surface of the chelipeds. Lobsters inhabiting

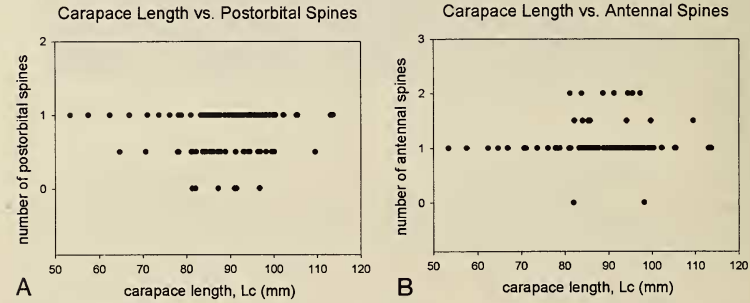


Fig. 4. Scatterplots comparing number of carapace spines with carapace length. Plots indicate that expression of spines is unrelated to age.

Table 3.—Frequency of expression of 0–4 lateral rostral spines in association with sexes and substrates.

# Rostral spines	Overall $n = 172$	Male $n = 88$	Female $n = 84$	Mud dweller $n = 44$	Rocky dweller $n = 31$
4	2%	2%	1%	5%	0%
3	45%	41%	50%	39%	42%
2	51%	56%	47%	52%	58%
1	1%	0%	2%	2%	0%
0	1%	1%	0%	2%	0%

Table 5.—Frequency of expression of 1–4 spines on lower margin of crusher claw in association with sexes and substrates.

# Spines on Cr-low	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
1	32%	29%	36%	32%	32%
2	48%	47%	50%	50%	49%
3	18%	21%	14%	18%	19%
4	2%	3%	0%	0%	0%

muddy bottoms have pristine lower claw surfaces, whereas lobsters inhabiting hard, rocky bottoms are badly abraded and scratched over this region (Fig. 2). Those inhabiting gravelly or shelly bottoms exhibit an intermediate condition.

The study area, being approximately 16 km in longest dimension, is small geographically, but the lobsters collected in this area range seasonally over a much larger region. Therefore, we think we are examining variation over an area comparable in size to the James Ross basin, Antarctica, which yielded the fossil *Hoploparia*.

Results and Discussion

General.—Detailed examination of 175 *H. americanus* indicates that carapace proportions, carapace groove positions, carapace spines and general claw form show only a small degree of variation (over the measured size range of individuals in the study area)—regardless of age, sex or substratum. These findings corroborate the generally held but scarcely published conclusion of taxonomists on modern lobsters: these features are essentially constant within species and, therefore, taxonomically useful at the species level. The number and arrangement of spines on the rostrum and claws are, however, variable within the species and, therefore, much less useful taxonomically. This variation is unrelated to age, sex or substratum.

Carapace proportions.—Over the measured size range of adult lobsters, all of the measured features on the carapace increase linearly with an increase in carapace length. These parameters include carapace height (Fig. 3A–B), width (Fig. 3C–D), length of the branchial region (Fig. 3E–F). distance between the orbit and prominence omega, and distance between prominence omega and the postcervical groove at the dorsomedian. The complete overlap of data plotted for males and females, and for dwellers on muddy and rocky substrata, indicates that neither sex nor substratum affects the proportions of the carapace or its regions.

Carapace spines.—On specimens of *H. americanus* from around Mt. Desert Island, the supraorbital spine is invariably present (100%; $n = 84$) and the postorbital and antennal spines are nearly always present in some form. These observations corroborate

Table 4.—Frequency of expression of 4–6 spines on upper margin of crusher claw in association with sexes and substrates.

# Spines on Cr-up	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
4	62%	58%	68%	61%	63%
5	32%	37%	23%	36%	28%
6	7%	5%	9%	3%	9%

Table 6.—Frequency of expression of 4–6 spines on upper margin of cutter claw in association with sexes and substrates.

# Spines on Cut-up	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
4	56%	54%	57%	52%	58%
5	41%	46%	33%	44%	39%
6	3%	0%	10%	4%	3%

Table 7.—Frequency of expression of 1–3 spines on lower margin of cutter claw in association with sexes and substrates.

# Spines on L-cut	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
1	54%	57%	50%	57%	53%
2	39%	38%	40%	41%	37%
3	7%	5%	10%	4%	10%

the observations of taxonomists of modern lobsters (Fenner Chace, Jr., Austin B. Williams, pers. comm.) that carapace spines are reliable diagnostic characters at the species level. The postorbital spine (Table 1) is usually small—much smaller than the supraorbital spine—and is almost always present (95%; $n = 148$), either as a distinct spine (66%) or a subtler, less pointed projection (29%). On a few specimens (9%, $n = 85$), the postorbital spine is expressed differently on the left and right sides of the carapace. The antennal spine (or spines) (Table 2) is almost invariably (99%; $n = 150$) present. although form varies in detail. It usually occurs as a single spine (84%), but also occurs as two spines of different size (7%), or as a pair of spines of equal size (8%). On some specimens (20%; $n = 85$), the antennal spine is expressed differently on the left and right sides of the carapace. Expression of the postorbital and antennal spines is independent of age (Fig. 4), sex or substratum (Table 8).

Lateral rostral spines.—Although not considered in the study of Antarctic *Hoploparia*, one of us (D.T.) has observed, in many other fossil lobsters, intraspecific or interspecific variation in the arrangement and number of spines on the rostrum and inner margins of the claws. Therefore, in this study, we examined variation in these features in *H. americanus*. The number of distinct lateral spines (smaller "spinules" not counted) on each side of the rostrum is variable ($n = 172$), but almost always either 2 (51%) or 3 (45%); 0 (1%), 1 (1%) or 4 (2%) spines occur rarely (Table 3). As with the carapace spines, variation in number of lateral rostral spines is unrelated to age, sex and substratum (Table 8). There is usually (88%; $n = 131$) an equal number of spines on each margin of the rostrum. The number of spinules posterior to these spines is highly variable and often unequal on left and right sides of the carapace.

Claw ornamentation.—Templeton (1935) documented that the claws of male *Homarus* are longer than claws of females of the same carapace length. There is no mention

Table 8.—Results of Chi-square test for independence of morphology from both sex and substratum. Cutoff value is for 95% confidence level. In all cases, calculated value is less than cutoff value, indicating that variation in these features is independent of sex or substratum.

Morphologic feature	Chi-square values for sex	Chi-square values for substratum
Postorbital spine	Calculated = 2.328 Cutoff = 5.991	Calculated = 4.216 Cutoff = 5.991
Antennal spine	Calculated = 1.481 Cutoff = 7.815	Calculated = 5.756 Cutoff = 7.815
Lateral rostral spines	Calculated = 4.838 Cutoff = 9.488	Calculated = 2.978 Cutoff = 9.488
Spines on cutter claw inner, upper margin	Calculated = 4.063 Cutoff = 5.991	Calculated = 0.095 Cutoff = 5.991
Spines on cutter claw inner, lower margin	Calculated = 0.539 Cutoff = 5.991	Calculated = 0.876 Cutoff = 5.991
Spines on crusher claw inner, upper margin	Calculated = 1.422 Cutoff = 5.991	Calculated = 1.035 Cutoff = 5.991
Spines on crusher claw inner, lower margin	Calculated = 1.260 Cutoff = 7.815	Calculated = 0.030 Cutoff = 7.815

in the literature, however, of intraspecific differences in claw shape or ornamentation. Claw shape was not formally evaluated in this study, but observations of hundreds of specimens revealed no obvious variation in claw shape. The surface of the claws in *H. americanus* is consistently smooth, regardless of age, sex or substratum. The number of spines on the inner margin of the palm (propodus) of both cutter and crusher claws is, however, variable, and therefore unsuitable for defining species (Tables 4–7). Variation in these spines is unrelated to age (Fig. 4), sex or substratum (Table 8).

Summary

Examination of 175 *H. americanus* indicates that carapace proportions, carapace groove positions, expression of carapace spines and general claw form are nearly constant on lobsters in the study area—regardless of age, sex or substrate. These findings corroborate the scarcely published conclusion of taxonomists on modern lobsters that these features are reliable species characters. This study also shows, however, that number and arrangement of spines on the rostrum and claws are variable within the species and, therefore, not good species characters; this variation is unrelated to age, sex or substratum.

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